A Model for Drosophila melanogaster Mating Behavior

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A MODEL FOR *DROSOPHILA MELANOGASTER* MATING BEHAVIOR

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During the last few decades much attention has been focused on mating behavior. Several kinds of mate choice have been suggested for *Drosophila*, including the rare-male advantage (for reviews, see, e.g., Spiess 1982; Knoppien 1985) and negative assortative mating (Averhoff and Richardson 1974). These two mechanisms could be responsible for the genetic polymorphism reported by Lewontin (1974). Another kind of mate choice leading to positive assortative mating, a mechanism by which speciation could start and be maintained, has been reported many times (see, e.g., Bryant et al. 1980; Ehrman and Parsons 1980).

Kence and Bryant (1978) pointed out the previous lack of a model characterizing and quantifying variation in mating behavior within and among populations or semi-species, and they provided one, based mainly on experience with *Musca domestica*. They proposed that if no sexual isolation exists between a male and a female, the copulation-latency time is given by the formula $X = H/(a_{\delta} - a_{\varphi})$, where X (copulation-latency time) is defined as the time between the introduction of the flies in the mating chamber and the start of copulation, H is a constant reflecting female threshold, and a_{δ} and a_{φ} are normally distributed stochastic variables describing the male and female sexual activities or vigors, respectively. The means and standard deviations of both these normal distributions were thought to be equal because of coevolution.

Bryant et al. (1980) used this *M. domestica* model to show that the rare-male advantage could be an artifact of wing clipping. Knoppien (1984), however, found that this was true only in special cases. Furthermore, Bryant (1979) pointed out, using the *M. domestica* model, that the negative assortative mating found by Averhoff and Richardson (1974) could be explained exclusively by interstrain differences of the means or standard deviations of their variables a_{δ} and a_{φ}. Later, Van den Berg et al. (1984) showed experimentally that this alternative explanation for the results of Averhoff and Richardson was the most parsimonious one.

In spite of the good qualitative fit for the results of Van den Berg et al., the *M. domestica* model needed to be revised in order to apply quantitatively to the mating behavior of *Drosophila melanogaster*. The shape of a histogram describing

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a number of copulation-latency times of single pairs of *D. melanogaster* does not fit the *M. domestica* model. The reasons for this are twofold.

1. When a_{σ} and a_{φ} are normally distributed with equal means and standard deviations, $H/(a_{\sigma} - a_{\varphi})$ is negative in 50% of single pairs. Thus, in this situation the mating percentage cannot exceed 50%. In *D. melanogaster*, however, single-pair mating percentages can be much higher, reaching nearly 100%. Although Bryant (1982) referred to percentages of 68% and 70%, Robertson (1982) reported a mating percentage of 92.9%. Because these percentages are always minimum estimates on account of the finite time the flies are allowed to court, Robertson's high estimate is probably the closest to the percentage that might be expected after infinite time.

2. In the *M. domestica* model, if the mean vigor of the males of one strain is x times that of another strain, the same can be said about the mean vigor of the two strains of the females. However, the results of Van den Berg et al. (1984) strongly indicated that this is invalid. These authors found that the male mating percentages varied much more than the female mating percentages, although in this setup the males, like the females, were allowed to copulate only once.

This paper describes a new model for fly mating behavior, incorporating Kence and Bryant's suggestion of using a threshold model and applying it to *D. melanogaster*. Such a threshold model can predict 100% matings for a number of single pairs, which is not far from the truth for *D. melanogaster*, and contrasts sharply with Kence and Bryant's model for *M. domestica*.

THE MODEL

"*Drosophila* courtship is best regarded as the means whereby a male provides a female with a stream of stimuli whose effects summate, finally reaching a critical level where she accepts him" (Manning 1967). The *D. melanogaster* model is in fact the mathematical equivalent of this statement. If X is the copulation-latency time of an arbitrary female and an arbitrary male, R is the reluctance of that female, and V is the vigor of that male, then the model postulates that $X = R/V$. The term reluctance is used because this is not the same as the variable female vigor as used by Kence and Bryant (1978).

If it is assumed that R and V are normally distributed stochastic variables, it must also be assumed that their means are large in comparison with their standard deviations (say, twice the size) in order to minimize the chance of negative values. However, the resulting distribution of X is not as strongly skewed and leptokurtic as the frequency distribution of actual copulation-latency times. Therefore, it is proposed that R and V are γ-distributed. These distributions only define chances for positive values. R has a γ-distribution with parameters α_1 and β_1. In short, $R \sim \gamma(\alpha_1, \beta_1)$ if the probability density function $f(r)$ is

$$f(r) = \frac{r^{\alpha_1 - 1} e^{-r/\beta_1}}{\beta_1{}^{\alpha_1}\Gamma(\alpha_1)} \quad \text{for } R \geq 0, \qquad f(r) = 0 \quad \text{for } R < 0, \tag{1}$$

where

$$\Gamma(\alpha_1) = \int_0^{\infty} y^{\alpha_1 - 1} e^{-y} dy .$$

Similarly, $V \sim \gamma(\alpha_2, \beta_2)$. For $\alpha_1 = 1$ the distribution is a negative exponential; for large α_1, the γ-distribution is approximately normal with $\mu = \alpha_1\beta_1$ and $\sigma = \alpha_1^{1/2}\beta_1$. The shape of the γ-distribution is described by α_1, and β_1 is a scaling parameter.

If $R \sim \gamma(\alpha_1, \beta_1)$ and $V \sim \gamma(\alpha_2, \beta_2)$, then according to Appendix A the probability density function of x for $X \geq 0$ is

$$p(x) = \frac{\Gamma(\alpha_1 + \alpha_2)}{\Gamma(\alpha_1)\Gamma(\alpha_2)} c^{\alpha_2} \frac{x^{\alpha_1 - 1}}{(x + c)^{\alpha_1 + \alpha_2}},$$

and for $X < 0$,

$$p(x) = 0. \tag{2}$$

This last distribution has three parameters: α_1 and α_2 (the original α's) describing the shape of the distribution, with c ($= \beta_1/\beta_2$, the original β's) as a scaling parameter. If one assumes that $\alpha_1 = \alpha_2 = \alpha$, it is possible (according to Appendixes B and C) to estimate c and α, even if the copulation-latency times greater than a certain value are unknown because of the experimental setup. The only requisite is that at least the median copulation-latency time and those times shorter than the median are known. The estimator for c ($= \tilde{c}$) is the median copulation-latency time, and that for α ($= \tilde{\alpha}$) is given by

$$\tilde{\alpha} = \frac{N/4}{\sum_{i=1}^{N} [(X_i^* - \tilde{c})/(X_i^* + \tilde{c})]^2} - \tfrac{1}{2}, \tag{3}$$

where N is the number of copulation-latency times, $X_i^* = X_i$ when $X_i < \tilde{c}$, and $X_i^* = \tilde{c}$ when $X_i \geq \tilde{c}$. X_i is the ith copulation-latency time.

TESTING THE MODEL

Single Matings

To test the model, single pairs of *Drosophila melanogaster* (Groningen strain) were kept for 1 h in a cylindrical mating chamber (2.3 cm in diameter, 7.8 cm in height). The copulation-latency times for 570 such pairs were recorded; 410 of these pairs (72%) mated within 1 h (results shown in fig. 1). To fit these data to the *D. melanogaster* model, α_1, α_2, and c were estimated numerically by varying α_1, α_2, and c independently to find the lowest χ^2 for a goodness-of-fit test. This best fit was found for α_1 and α_2, giving approximately equal shapes for the underlying probability density functions of R and V. Therefore, α_1 and α_2 were assumed to be equal, and the above-mentioned estimators for α and c were applied, resulting in $\tilde{c} = 27$ min and $\tilde{\alpha} = 1.526$. A χ^2 test for goodness of fit (including the "remainder," or the copulation-latency times longer than 1 h) resulted in $\chi^2_{10} = 10.395$ ($P = .407$), suggesting a good fit.

It is obvious that the *Musca domestica* model with its 50% mating constraint will not fit these data, if only because 72% of the *Drosophila* were mated within 1 h. Kence and Bryant suggested, however, that in some cases the 50% constraint does not apply because, in contrast to their primary assumption, mean male vigor

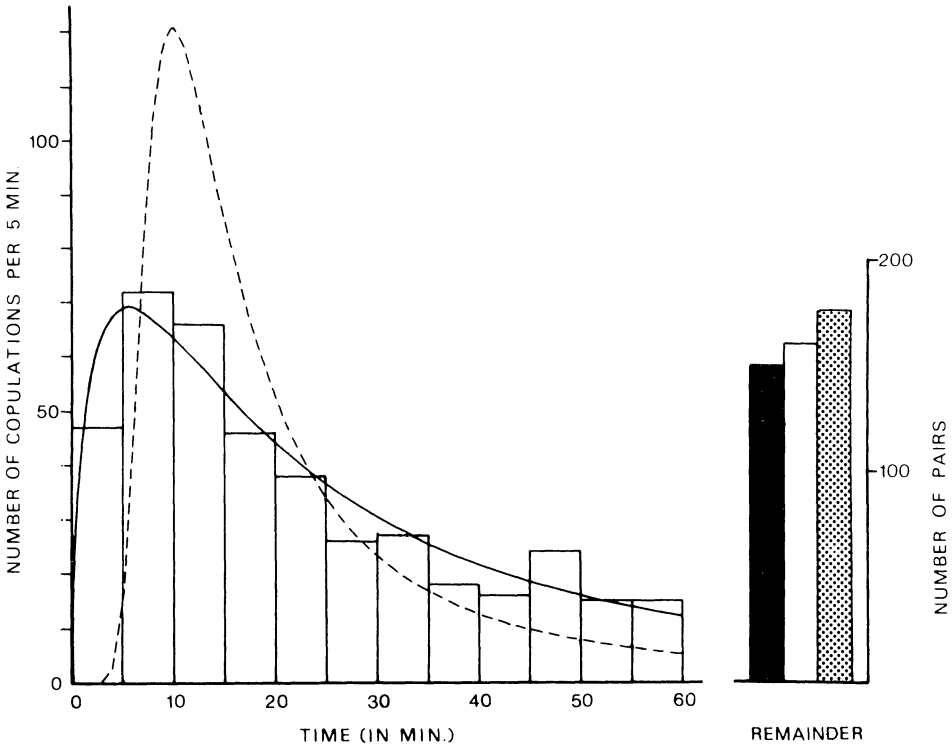

FIG. 1.—Frequency distributions of copulation-latency times and the number of remaining (noncopulating) pairs: open columns, experimental values; solid line and black column for the remainder, the values predicted by the *D. melanogaster* model; dashed line and dotted column for the remainder, the values predicted by the modified *M. domestica* model.

might be greater than mean female vigor. In that case, the two important parameters are $\Delta\mu$ and σ ($\Delta\mu$ is the mean male vigor minus mean female vigor). For my data $\Delta\mu$ was estimated as 0.04354 and σ as 0.03797 (both in what Kence and Bryant called "standard units of vigor"). To estimate these parameters, I used a method like that described by Kence and Bryant (1978, p. 1052), but because there are two parameters, at least two percentiles have to be used (in this case, the 33.3 and the 66.7 percentiles). The expected curve of this modified *M. domestica* model is also shown in figure 1. The test for the goodness of fit gave a χ^2_9 (only nine degrees of freedom because the first two classes had to be combined) of 97.324, which is highly significant. This bad fit is also illustrated clearly by figure 1.

I used data from the literature to test the general utility of the model in giving a good prediction of copulation-latency times in the single-pair situation. Only Robertson's (1982) data gave enough detail to allow this. I calculated 465 copulation-latency times from his figure 4. Although Robertson distinguished between male latency (or lag) and courtship duration, both are included in copulation-latency time according to the definition used here. I estimated $\bar{\alpha}$ and $\bar{c}$ as 4.31 and 84 s, respectively. I found only 465 points, not 492 as claimed by Robertson. It

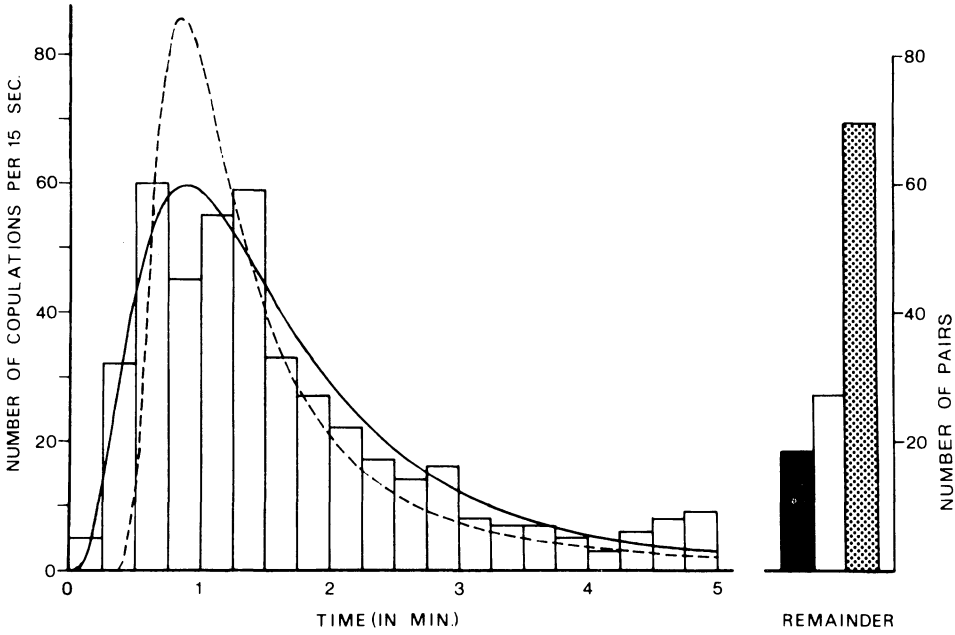

FIG. 2.—Frequency distributions of copulation-latency times and the number of remaining (noncopulating) pairs: open columns, values from Robertson 1982; solid line and black column for the remainder, the values predicted by the *D. melanogaster* model; dashed line and dotted column for the remainder, the values predicted by the modified *M. domestica* model.

was assumed that these 465 were a random sample from the original 492. Figure 2 illustrates clearly that here too the *D. melanogaster* model fitted well. Again, the revised *M. domestica* model gave a bad fit ($\chi^2_{15} = 215.41$). The χ^2_{17} value for a goodness-of-fit test was 37.63 for the *D. melanogaster* model. This highly significant but nevertheless small deviation from the model was caused mainly by the extreme right tail of the distribution. Thus, for some unknown reason a small proportion of the pairs (4%–5%) had longer than expected copulation-latency times.

Mass-Mating Experiments

Here the *D. melanogaster* model was used to explain the mass-mating results of Van den Berg et al. (1984), particularly the significant deviations from random mating. They proved that the Kence and Bryant model qualitatively, at least, gave a reasonable explanation for these deviations.

Four strains were used in these mass-mating experiments: Israel (I), Bogota (B), Pacific (P), and Groningen (G). All six possible combinations of two strains were tested by a method similar to that of Averhoff and Richardson (1974). Five individuals per sex and per strain were introduced in a mass-mating chamber and observed continuously for 1 h. When a copulation occurred, the mating flies were removed and identified, and the time of copulation was recorded. Table 1 shows

TABLE 1

OBSERVED MATING PATTERNS FOR EACH COMBINATION OF TWO STRAINS (A AND B) OF FOUR AND χ^2 TESTS FOR DEPARTURES FROM RANDOM MATING, FOR MATING PERCENTAGES, AND FOR ASSORTATIVE MATING

STRAIN		TYPE OF MATING(♂ × ♀)						χ^2 tests[d]			
A	B	A×A[a]	A×B[a]	B×A[a]	B×B[a]	NC[b]	N[c]	Departure from Random Mating	Male Mating Percentage	Female Mating Percentage	Assortative Mating
I	B	18.5	10.1	16.2	15.8	39.4	297	7.51	0.56	3.76	3.20
I	P	15.4	11.1	18.2	15.0	40.4	280	4.86	2.16	2.64	0.05
I	G	13.5	9.5	21.7	7.9	47.4	304	26.35**	2.50	18.23**	5.63*
B	P	14.4	12.7	13.3	13.3	46.4	362	0.39	0.02	0.19	0.19
B	G	18.4	5.9	16.8	11.2	47.7	375	28.04**	1.00	23.59**	3.45
P	G	13.9	9.9	16.3	10.9	49.1	375	7.43	0.88	6.41*	0.13

NOTE.—Strains: B, Bogota; G, Groningen; I, Israel; P, Pacific.

[a] Percentages for each mating type.

[b] Percentage of those not copulating (100% minus the percentage of actual copulations).

[c] Number of possible copulations.

[d] For the test for random mating, 3 degrees of freedom; 1 degree of freedom for the other tests.

* $P < .05$.

** $P < .001$.

the results and indicates occurrences and types of significant deviations from random mating.

These experiments were simulated by assuming that five individuals of each sex and of each of two strains were placed in a mass-mating chamber, as in the real experiments. Random values, indicating individual vigor or reluctance were drawn from a $\gamma(\alpha, \beta)$-distribution. The β value varied between sexes and strains, but α was constant for all sexes and strains at 1.5, very close to the estimated value of the single-mating experiments. By means of three random numbers (u_1, u_2, u_3) from a standard normal distribution, I took a random number Z, defined as $\frac{1}{2}\beta(u_1^2 + u_2^2 + u_3^2)$, from a $\gamma(1.5, \beta)$-distribution.

The males and females were paired randomly. A pair was removed immediately after they started to copulate. All the remaining males and females were again paired randomly after such a removal, in order to simulate the changing contacts that occur in reality. If a male was randomly paired with a female being courted by another male, I assumed that the most vigorous male usurped all the accumulated courtship of the other less vigorous male(s).

The program also allows male polygamy, including adjustable copulation durations, and contains the same expression for isolation between distinct genotypes used by Kence and Bryant. In the simulation used here, however, these options were not applied. The program is written in Pascal and was executed on a Data Control Cyber 170/760 (it is available from the author upon request).

Using the program, four different values for β must be introduced: one for each sex and strain. The β's indicating male vigors were always part of the series $\{2^{i/4}; i = 1, 2, \ldots, 12\}$, and the β's indicating female reluctance were always part of the series $\{1250.2^{i/4}; i = 1, 2, \ldots, 12\}$. The former are expressed in courtship units per

TABLE 2

VALUES OF THE β'S ASSIGNED TO THE EIGHT SEXES AND STRAINS, WHICH RESULTED IN SIMULATED DATA THAT BEST FITTED THE EXPERIMENTAL DATA

STRAIN	I	B	P	G
β of male vigor	1.00	1.41	1.19	1.68
β of female reluctance	1768	2973	3536	7071

NOTE.—Strains are abbreviated as in table 1.

TABLE 3

SIMULATED MATING PATTERNS FOR EACH COMBINATION OF TWO STRAINS (A AND B) OF FOUR

STRAIN		TYPE OF MATING (♂ × ♀)				
A	B	A×A[a]	A×B[a]	B×A[a]	B×B[a]	NC[b]
I	B	18.4	11.7	19.4	16.0	34.5
I	P	18.6	11.3	19.4	13.4	37.3
I	G	15.4	8.0	22.3	8.6	45.7
B	P	15.9	14.0	13.3	12.7	44.1
B	G	18.7	8.2	16.5	11.8	44.8
P	G	14.4	7.7	16.8	11.1	50.0

NOTE.—Patterns are computed using the values for the eight β's as given in table 2. The number of possible copulations for each combination is 1000. Strains are abbreviated as in table 1.

[a] Percentages for each mating type.

[b] Percentage of those not copulating (100% minus the percentage of actual copulations).

second, whereas the latter are expressed in courtship units. Every combination of four β's was repeated 100 times, and the resulting mating patterns were stored. The maximum time allowed to copulate was 3600 s.

The simulated data including the noncopulatory classes were compared to the real data in order to estimate which values of the β's assigned to the eight sexes and strains gave the best fit. The combination of β's that gave the best fit with the practical data (the lowest χ^2 value) is given in table 2. Using these β's, the simulated mating patterns for the six combinations were as given in table 3.

The χ^2 value obtained when comparing the simulated data of the IB combination with the real data was 3.35; for IP the value was 2.40, for IG 1.55, for BP 1.11, for BG 2.59, and for PG 1.70. This gives a total χ^2 of 12.70 for all the combinations together. When no parameters would have been estimated, a χ^2 value of one combination would have 4 degrees of freedom, resulting in 24 degrees of freedom for the total χ^2. However, seven of these β's were estimated during the search for the lowest χ^2 value, leaving finally 17 degrees of freedom. The results of the simulations are not determined by the absolute values of the β's, but by their relationships. Therefore, one such β was arbitrarily chosen (β for the male vigor of Israel was set to 1) and did not have to be estimated. The conclusion is evident: the real results correspond well to the simulated ones. This shows that all the significant deviations from random mating, as found by Van den Berg et al.,

including the negative assortative mating, can be explained fully in terms of interstrain differences in male vigor and female reluctance.

DISCUSSION

Evidence in the literature shows that a female summates courtship behaviors until she reaches a certain critical level and accepts the males' copulation attempts. Ewing (1964), for instance, found a linear positive relationship between the percentage of male wing surface kept intact and the number of copulations. This indicates that the stimulus provided by wing vibrating is summated by the female. Cook (1973) and Crossley and McDonald (1979) showed that the amount of male courtship an individual female requires before accepting copulation is fairly constant, suggesting that a threshold mechanism is involved. Schilcher (1976) was able to decrease the copulation-latency time by simultaneously stimulating females with pulse song during male courtship. Furthermore, he was also able to obtain a decrease by pre-stimulating females with artificial sine song, indicating that a female can store and "remember" this aspect of male courtship.

Robertson (1982), however, objected to this idea of female courtship summation. He claimed that several of his data left this idea largely unsupported. First, he could find only a negative correlation between mating speed and pulse song but not sine song; furthermore, this relation was weak. Weak relations might be expected, however, when one attempts to correlate only one of many possible aspects of courtship with courtship duration, in which many cues are probably involved.

Second, Robertson was unable to verify that a female requires a fairly constant amount of courtship, as established by Cook (1973) and Crossley and McDonald (1979). Closer examination of the data of the different authors reveals that Robertson found the same global trends, though he did not find these trends to be significant.

Robertson believed that the long courtship durations were not due to summation and suggested an alternative explanation based on the hyperbolic relation he found between male latency (the time between introduction and first courtship) and courtship duration (time between first courtship and copulation). He explained this relation as follows. Most females need a certain time after introduction to quiet down before responding to male courtship. When a male starts courting immediately upon introduction, the courtship time will be long because no success will be achieved before the female is ready. If the male does not begin courtship before the female is ready, this effect will be absent, resulting in a short courtship.

It is not necessarily correct to assume that during the period of what he called male latency, the male is not a passive source of courtship signals, such as visual stimuli (Willmund and Ewing [1982] gave evidence for the existence of such stimuli) or perhaps pheromones. Such courtship signals may already be present during the male latency period. One way of avoiding this difficulty is to define copulation-latency time as male latency plus courtship duration. When this definition was used, the *Drosophila melanogaster* model fitted very well. The only

exception is that the number of copulation-latency times longer than ±270 s was a bit higher than expected. Robertson reported that a small group of his females seemed to become very agitated because of the constant male courtship, resulting in a "curling" rejection response by these females and consequently long courtships. It is possible that this special group of females is responsible for the deviation found in figure 2.

To my knowledge, two mathematical descriptions for insect mating behavior involving copulation-latency times have been published: Taylor's (1975) model, and Kence and Bryant's (1978). Taylor's model is essentially a collision model and is only applicable when courtship duration is much shorter than the time that mating partners need to find each other, which is not the case here. I have also shown here that the Kence and Bryant *Musca domestica* model is not applicable to *D. melanogaster*. Conversely, it is unlikely that the *D. melanogaster* model can explain the mating results of *M. domestica*, since Kence and Bryant stated (1978, p. 1058) that many single pairs never seem to mate, a condition not to be expected with the *D. melanogaster* model. Although an accurate check is not possible because the authors did not publish the number of pairs used for their single-mating experiments, it is possible to construct a universal model.

Kence and Bryant stated that copulation-latency time is $H/(a_{\sigma} - a_{\varphi})$. Where H reflects the initial female threshold and is assumed to be constant, a_{σ} and a_{φ} reflect the male and female sexual activity or vigor, respectively, and are normally distributed. In the *D. melanogaster* model, H is female reluctance (R), and a_{σ} is male vigor (V). It follows that in a universal model, copulation-latency time is $R/(V_{\sigma} - V_{\varphi})$ where $R \sim \gamma(\alpha_1, \beta_1)$, $V_{\sigma} \sim \gamma(\alpha_2, \beta_2)$, and $V_{\varphi} \sim \gamma(\alpha_3, \beta_3)$. When α_1, α_2, and α_3 are large, these distributions would be practically normal, and if $\alpha_2 = \alpha_3$ and $\beta_2 = \beta_3$, the denominator would have a relatively high variance and zero mean, whereas the numerator would have a high mean ($\alpha_1\beta_1$) compared to its standard deviation ($\beta_1\sqrt{\alpha_1}$). In such a situation the standard deviation of the numerator hardly influences the resulting distribution of the copulation-latency times; thus, in this case R can safely be considered a constant. Application of these assumptions gives a transformation into the *M. domestica* model.

A transformation into the *D. melanogaster* model is achieved by assuming that V_{φ} is zero. V_{φ} causes the ultimate mating percentage to be lower than 100%; the higher that V_{φ} is compared to V_{σ}, the lower this percentage will be. Since the mating percentage can reach nearly 100% in *D. melanogaster*, V_{φ} is probably negligible compared to V_{σ}. Given that V_{φ} is the crucial element underlying the difference between the *D. melanogaster* and *M. domestica* models, it is interesting to try to identify the behavioral equivalent of V_{φ}. Given that V_{φ} lengthens the copulation-latency time, the behavioral mechanisms or signals analogous to V_{φ} must be sought in the female rejection responses, rather than in signals or behavior involved in attracting the male. Two categories of rejection responses are present: moving away, and other kinds of rejection such as wing flicking or kicking (for a full description, see, e.g., Connolly and Cook 1973).

When a female moves away, the accumulated courtship might be "forgotten" by the female. Schilcher (1976) showed, however, that after playing sine song to a

single female, minutes later she is more ready to mate with a "deaf mute" male than after hearing white noise. Presumably, then, a female *Drosophila* remembers and stores this kind of courtship. When a female rejects without moving away, she might be able to influence the male by diminishing or altering his courtship. However, Wood and Ringo (1981), using *Drosophila melanogaster* and *D. simulans*, found that female behavior had little influence on male behavior. Connolly and Cook (1973), in analyzing this influence, showed that after a 3–4-day-old virgin female kicks (the predominant rejection response in this situation), the male changes from wing vibration to orientation. This effect was, however, short-lived and therefore probably negligible. Although it is unlikely that these two rejection behaviors contribute to the variable V_{φ} in *Drosophila*, they may be involved in V_{φ} in the mating behavior of other fly species.

There is also another relevant consequence of female rejection responses. When a female moves away, male courtship stops; the male is thus able to court for only a certain fraction (f) of the total time. Therefore, in terms of the model, more time is needed before the female reaches her threshold level. By multiplying male vigor by the fraction f, this effect reduces male vigor and therefore cannot be interpreted as V_{φ}.

It is common knowledge that copulation-latency times are longer when bigger mating chambers are used, because the females can avoid the males more easily and more effectively.

The *D. melanogaster* model is a modification of the *M. domestica* model criticized by Spiess and Dapples (1981). The *D. melanogaster* model is constructed in such a way that many of their criticisms are no longer applicable. I do not assume that the female threshold (called reluctance here) is constant or that the variables used are strongly correlated and coevolved. Spiess and Dapples also criticized the description of complex behaviors, particularly female vigor, with a single symbol. In this study male vigor and female reluctance are described with a single symbol, but female vigor is not. This is indeed a simplification, and Spiess and Dapples are correct in stating that such a model cannot help to clarify the subtle behavioral mechanisms behind courtship. The model can be a valuable tool when care is taken that oversimplification has not taken place. The model presented here does not clarify the behavioral mechanisms behind courtship, but it does provide a mathematical framework that can be used to determine whether deviations from random mating are merely the result of differences in male vigor and female reluctance, or if more complex explanations are necessary. The model has already proved to be useful in this last respect.

SUMMARY

In 1978 Kence and Bryant developed a model for fly mating behavior, which proved to be unsatisfactory in describing *Drosophila* mating behavior. Here a new model is developed. Copulation-latency time is thought to be the quotient of two γ-distributed variables, female reluctance and male vigor. When two parameters are assumed to be equal, it is possible to derive estimators for the relevant

parameters of the distribution of the quotients. The model describes copulation-latency times of single pairs and the data of mass-mating experiments very well. Therefore, the model fully describes the deviation from random mating found earlier (Van den Berg et al. 1984). Furthermore, it gives a good fit for the data of Robertson (1982). Finally, it is shown that both Kence and Bryant's model and that described here can easily be interpreted as special cases of a simple universal model.

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APPENDIX A

Derivation of the Probability Density Function of the Copulation-Latency Times

If both the stochastic variables R and V are defined only for positive values and if $X = R/V$, then (according to Kendall and Stuart 1963, p. 265) the probability density function (PDF) of X is

$$\int_0^\infty f_1(xv)\, f_2(v)\, v\, dv \qquad \begin{matrix} f_1(xv) \text{ is the PDF for } R \\ f_2(v) \text{ is the PDF for } V. \end{matrix} \tag{A1}$$

Therefore, if $R \sim \gamma(\alpha_1, \beta_1)$ and $V \sim \gamma(\alpha_2, \beta_2)$, the PDF of X equals

$$\int_0^\infty \frac{(xv)^{\alpha_1 - 1} e^{-xv/\beta_1}}{{\beta_1}^{\alpha_1}\, \Gamma(\alpha_1)} \frac{v^{\alpha_2 - 1} e^{-v/\beta_2}}{{\beta_2}^{\alpha_2}\, \Gamma(\alpha_2)}\, v\, dv =$$

$$\frac{x^{\alpha_1 - 1}}{{\beta_1}^{\alpha_1}{\beta_2}^{\alpha_2}\, \Gamma(\alpha_1)\, \Gamma(\alpha_2)} \int_0^\infty v^{\alpha_1 + \alpha_2 - 1} e^{-[(\beta_1 + \beta_2 x)/\beta_1\beta_2]v} dv\,. \tag{A2}$$

The part of equation (A2) following the integral sign in the right-hand side is itself related to a γ-distribution. Using this, it can easily be seen that the value of the integral is

$$\Gamma(\alpha_1 + \alpha_2)\, [\beta_1\beta_2/(\beta_1 + \beta_2 x)]^{\alpha_1 + \alpha_2}.$$

Therefore, the PDF of X is

$$\frac{\Gamma(\alpha_1 + \alpha_2)}{\Gamma(\alpha_1)\, \Gamma(\alpha_2)\, {\beta_1}^{\alpha_1}{\beta_2}^{\alpha_2}} x^{\alpha_1 - 1} \left(\frac{\beta_1\beta_2}{\beta_1 + \beta_2 x}\right)^{\alpha_1 + \alpha_2} =$$

$$\frac{\Gamma(\alpha_1 + \alpha_2)}{\Gamma(\alpha_1)\, \Gamma(\alpha_2)} \frac{{\beta_1}^{\alpha_2}}{{\beta_2}^{\alpha_2}} \frac{x^{\alpha_1 - 1}}{[x + \beta_1/\beta_2]^{\alpha_1 + \alpha_2}} \tag{A3}$$

This leads to the PDF given in the main text when $\beta_1/\beta_2 = c$.

APPENDIX B

Derivation of an Estimator for c When $\alpha_1 = \alpha_2 = \alpha$

It will be proved that $F(c) = \frac{1}{2}$ if $\alpha_1 = \alpha_2 = \alpha$, indicating that the sample median ($= \tilde{c}$) is a plausible estimator for c:

$$F(c) = \int_0^c \frac{\Gamma(2\alpha)}{\Gamma(\alpha)\,\Gamma(\alpha)}\, c^{\alpha}\, \frac{x^{\alpha-1}}{(x+c)^{2\alpha}}\, dx . \tag{B1}$$

Substituting $u = x/(x + c)$, this becomes

$$\int_0^{1/2} \frac{\Gamma(2\alpha)}{\Gamma(\alpha)\,\Gamma(\alpha)}\, c^{\alpha}\, \frac{[cu/(1-u)]^{\alpha-1}}{[c/(1-u)]^{2\alpha}}\, \frac{c}{(1-u)^2}\, du =$$

$$\int_0^{1/2} \frac{\Gamma(2\alpha)}{\Gamma(\alpha)\,\Gamma(\alpha)}\, u^{\alpha-1}\,(1-u)^{\alpha-1} du . \tag{B2}$$

The expression following the integral sign is the PDF of a $\beta(\alpha, \alpha)$-distribution, which is defined for $0 \leq U \leq 1$ and is symmetrical around $\frac{1}{2}$. Using this, it can easily be seen that the right-hand side of equation (B2) reduces to $\frac{1}{2}$. Hence, $F(c) = \frac{1}{2}$.

APPENDIX C

Derivation of an Estimator for α When $\alpha_1 = \alpha_2 = \alpha$

From Appendix B it is clear that if $U = X/(X + c)$, U follows a $\beta(\alpha, \alpha)$-distribution. According to Fisz (1958, pp. 137–138),

$$E(U^n) = \Gamma(2\alpha)\,\Gamma(\alpha + n) \,/\, \Gamma(\alpha)\,\Gamma(2\alpha + n) \tag{C1}$$

$$E(U) = \tfrac{1}{2} \qquad \text{and} \qquad E(U^2) = (\alpha + 1)/(4\alpha + 2) . \tag{C2}$$

Hence,

$$\sigma^2(U) = 1/(8\alpha + 4) \qquad \text{or} \qquad \alpha = [1 - 4\sigma^2(U)]/8\sigma^2(U) . \tag{C3}$$

The moment estimator for α ($= \tilde{\alpha}$) is, therefore,

$$[1 - 4s^2(U)]/8s^2(U) \qquad \text{where} \qquad s^2(U) = \frac{1}{n}\sum_{i=1}^{n} (U_i - \tfrac{1}{2})^2 . \tag{C4}$$

But if the X's greater than a constant are not known, neither are the U's greater than another constant. Therefore, $s^2(U)$ cannot be calculated. However, given the fact that the PDF of U is symmetrical around $\frac{1}{2}$, another estimator for $\sigma^2(U)$ is

$$\frac{2}{n}\sum_{i=1}^{n} (U_i^* - \tfrac{1}{2})^2 = s^2(U)^* , \tag{C5}$$

where n is the total number of copulation-latency times, and $U_i^* = U_i$ when $U_i < \frac{1}{2}$ and $U_i^* = \frac{1}{2}$ when $U_i \geq \frac{1}{2}$. However, U is defined as $X/(X + c)$, whereas c is not known. Therefore, I propose $\tilde{c}$, the estimator for c, to be used to calculate U. Estimating α is this way requires three steps:

transforming all the X_i's into U_i's using the formula $U_i = X_i/(X_i + \tilde{c})$;
calculating $s^2(U)^*$ using formula (C5); and
calculating $\hat{\alpha}$ (the estimator for α) using the formula $\hat{\alpha} = [1 - 4s^2(U)^*]/8s^2(U)^*$.

Executing these three steps results in the formula given in the main text.

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